ZooKeys 1178: 279–291 (2023)
DOI: 10.3897/zookeys.1178.107007

Research Article

Species richness and endemism patterns of Sternorrhyncha (Insecta, Hemiptera) in China

Zhengxue Zhao[1], Xueli Feng[1], Yubo Zhang[1], Yingjian Wang[1], Zhengxiang Zhou[1], Tianlei Liu[1]

1 *College of Agriculture, Anshun University, Anshun, China*
Corresponding author: Zhengxue Zhao (zzx611324@163.com)

Abstract

One of the main goals in biogeography and ecology is the study of patterns of species diversity and the driving factors in these patterns. However, such studies have not focused on Sternorrhyncha in China, although this region hosts massive species distribution data. Here, based on the 15,450 distribution records of Sternorrhyncha species in China, we analyzed patterns in species richness and endemism at 1° × 1° grid size and determined the effects of environmental variables on these patterns using correlations analysis and the model averaging approach. We found that species richness and endemism of Sternorrhyncha species are unevenly distributed, with high values in the eastern and southeastern coastal regions of mainland China, as well as Taiwan Island. Furthermore, the key factors driving species richness and endemism patterns are inconsistent. Species richness patterns were strongly affected by the normalized difference vegetation index, which is closely related to the feeding habits of Sternorrhyncha, whereas endemism patterns were strongly affected by the elevation range. Therefore, our results indicate that the range size of species should be considered to understand the determinants of species diversity patterns.

Key words: Biogeography, ecology environmental variables, normalized difference vegetation index, phytophagous insect, species richness

OPEN ACCESS

Academic editor: Yalin Zhang
Received: 26 May 2023
Accepted: 18 August 2023
Published: 7 September 2023

ZooBank: https://zoobank.org/DDD2D2C4-82D6-4FDA-98EF-FF88F7DA32A7

Citation: Zhao Z, Feng X, Zhang Y, Wang Y, Zhou Z, Liu T (2023) Species richness and endemism patterns of Sternorrhyncha (Insecta, Hemiptera) in China. ZooKeys 1178: 279–291. https://doi.org/10.3897/zookeys.1178.107007

Copyright: © Zhengxue Zhao et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Macro-scale patterns of species richness are central to many fundamental questions in ecology and biogeography (MacArthur 1972; Huston 1994; Rosenzweig 1995). Species richness is unevenly distributed across a region (Gaston 2000), which means that some areas within a region have high species richness while others have low species richness. Exploring these patterns has fascinated ecologists and biogeographers for decades (Lobo et al. 2002; Qian et al. 2009a; Feng et al. 2016) and it is critical for understanding species evolution and developing conservation strategies (Pennisi 2005; Zhang et al. 2015; Zhao et al. 2016). While previous studies have found that energy availability is the most important factor in determining species richness patterns (Currie 1991; Hawkins et al. 2003), subsequent studies have reported other factors as more important (Araújo et al. 2008; Li et al. 2019; Lyu et al. 2020). Therefore, there is currently disagreement about the relative contributions of environmental factors, but it is believed that multiple environmental factors interact to influence

the patterns of species richness (Wang et al. 2012). Interestingly, several studies have found that the impact of environmental variables on species diversity patterns depends on the range size of species (Svenning and Skov 2007; Liu et al. 2017). Specifically, richness patterns of species are strongly affected by modern environmental factors, whereas those of range-restricted species (also known as endemic species) are strongly affected by historical climate change or topographic heterogeneity (Schuldt and Assmann 2009; Liu et al. 2017; Sosa and Loera 2017). Therefore, we must consider the range size of species to fully understand the causes and mechanisms of patterns of species richness (Schuldt and Assmann 2009).

In comparison to vertebrates and plants, relatively few studies have been conducted on the species richness pattern of insects, despite the fact that insects have the most species (Diniz-Filho et al. 2010; Economo et al. 2018). Thus, the key to revealing the underlying mechanism of global biodiversity is to strengthen the research on the formation mechanism of insect diversity patterns. The Sternorrhyncha suborder, a tiny sucking phytophagous insect of Hemiptera, consists of approximately 18,700 species worldwide (Drohojowska et al. 2020). This suborder comprises four groups: aphids, scale insects, whiteflies and psyllids. The Sternorrhyncha is highly morphologically diverse and widely thought to be of a monophyletic lineage (Drohojowska et al. 2020). Many Sternorrhyncha insects, such as *Myzus persicae* (Sulzer, 1776), *Dysmicoccus brevipes* (Cockerell, 1893) and *Phenacoccus madeirensis* Green, 1923, are major agricultural pests and invasive species. However, some species are beneficial to humans in various ways. Scale insects, for example, provide many useful materials such as red dyes, waxes, resins and medicines (Kondo et al. 2018). Furthermore, many Sternorrhyncha species have become biological indicators of zoogeographical regions and model taxa (e.g., aphids) for biogeography research (Wang et al. 2017). To date, studies on Sternorrhyncha have primarily focused on taxonomy and the prediction of potential distribution areas of some invasive species under climate change (Wei et al. 2019, 2020), but macro-scale patterns of species diversity and the underlying driving factors of these patterns have not been thoroughly investigated, particularly in China, which has the one of largest number of Sternorrhyncha species (Liu et al. 2009; Li 2011; Wei et al. 2016; Yan and Bai 2017).

Some researchers have investigated the species diversity patterns of all Sternorrhyncha in specific regions of China, or some taxa of Sternorrhyncha throughout China. Liu et al. (2009), for example, investigated the distributional patterns of aphid diversity in China using the inverse distance-weighted method. This study, however, did not quantify the effects of environmental factors on species distribution patterns. Wei et al. (2016) discovered that current climate is a major determinant of scale insect diversity patterns in China. Li et al. (2019) investigated the species richness patterns of Hemipteran insects and their relationships with environmental factors in the Qinghai-Tibetan Plateau, identifying climate change since the Last Glacial Maximum and habitat heterogeneity as the main driving factors for Sternorrhyncha. As previously stated, while some research has been conducted in China on the causes of Sternorrhyncha richness patterns, it is still insufficient to fully understand in the entire region. Thus, there is a pressing need to examine species diversity patterns using current popular methods. Further research on the factors influencing Sternorrhyncha

species diversity patterns in China will help shed light on the general explanation for the patterns of insect species diversity.

This paper aims to (1) analyze the species richness and endemism patterns of Sternorrhyncha in China, and (2) investigate the effects of multiple environmental variables on two types of patterns.

Material and methods

Geographic distribution patterns

A total of 15,450 distribution records of Sternorrhyncha species were obtained from previous studies (Gao 2018; Du et al. 2020; Li et al. 2021) and the Global Biodiversity Information Facility (https://www.gbif.org/). Species richness and endemism patterns were mapped by calculating the species numbers and weight endemism values in 1° × 1° grids, respectively. The weighted endemism of a grid was calculated as the sum of the range-down-weighted species values after each species was down-weighted by the number of grids in which it was found (Linder 2001). A grid size of 1° × 1° was chosen because it had been frequently used in previous studies on insect diversity patterns in China (Zhao et al. 2020a, 2021). We eliminated grids with less than half of their area in this study.

Environmental variables

Thirteen environmental variables were selected to identify key ecological factors that drive patterns of species richness and endemism and they were grouped into six categories as follows: 1) ambient energy: mean annual temperature (MAT) and annual potential evapotranspiration (PET); 2) water availability: mean annual precipitation (MAP) and annual actual evapotranspiration (AET); 3) climate seasonality: temperature annual range (TAR), temperature seasonality (TS), and precipitation seasonality (PS); 4) habitat heterogeneity: elevation range (ER, calculated by maximum elevation minus minimum elevation in 1° grid) and slope (SP); 5) productivity: normalized difference vegetation index (NDVI) and net primary productivity (NPP); and 6) historical climate stability: MAT change and MAP change; these two variables were defined as the absolute value of the difference between the current MAT/MAP and the Last Glacial Maximum MAT/MAP. Because past climate models were uncertain, MAT and MAP in the Last Glacial Maximum were calculated as the mean of the Model for Interdisciplinary Research on Climate Earth system (MIROC-ESM) and Community Climate System Model v.4 (CCSM4) models.

TAR, TS, PS, and MAT and MAP at present and Last Glacial Maximum were obtained from the WorldClim database (http://www.worldclim.org). The NDVI and NPP were obtained from the Resource and Environment Data Cloud Platform (http://www.resdc.cn/). The PET and AET were downloaded from the CGIAR-CSI database (http://www.cgiar-csi.org). Elevation data were obtained from CGIAR SRTM (http://srtm.csi.cgiar.org/). The spatial resolutions of NDVI and NPP were 1 km^2 and that of MAT and MAP in the Last Glacial Maximum was 2.5 arc min (~5 km). The spatial resolutions of other environmental variables were 30 arc-seconds (~1 km). Environment variable values were obtained in a 1° grid by calculating the mean of all pixels within it using ArcGIS v.10.5 (ESRI, Redlands, CA, USA).

Statistical analysis

The reliability of the relationship between species diversity and environmental variables is affected by sampling bias. As a result, assessing sampling bias is an unavoidable step in biogeography. Based on previous studies, a linear regression model was developed using the square-root-transformed number of records and the observed richness in a 1° × 1° grid (Zhao et al. 2020b, 2021). The degree of sampling bias is indicated by the ratio of the observed species richness to the predicted species richness obtained from the linear regression model.

Pearson correlation analysis was used to assess the relationships between species richness/endemism and each environmental variable. Spatial autocorrelation is frequently found in data on species richness, increasing the rate of a type I error in a significance test (Diniz-Filho et al. 2003). To solve this problem, Dutilleul's method was applied to estimate the number of degrees of freedom in correlation significance using Spatial Analysis in Macroecology v.4.0 software (Dutilleul et al. 1993; Rangel et al. 2010). Generally, the lowest value of the Akaike's information criterion (AIC) was considered the best model to assess the relationship between species diversity and environmental variables. However, AIC is sensitive to the presence of spatial autocorrelation and produces minimum adequate models that are unstable and overfitted (Diniz-Filho et al. 2008). Therefore, a model averaging approach based on Akaike weights was used to obtain relative roles of environmental variables, and they were performed in R v.3.6.1 using the MuMIn packages (Bartón 2018; R Core Team 2019). To reduce the collinearity between the environmental variables, three environmental variables with high variance inflation factors, including, AET, TS, and MAT change, were excluded in the model averaging process. The variance inflation factors of the remaining environmental variables were less than 15. All possible environment variable combinations were considered to build models, and the relative role of each environment variable was defined as the sum of the AIC weights for all models in which it appeared. Species richness and endemism were log10-transformed, and all variables were standardized (mean = 0 and standard deviation = 1).

Results

All distribution records of Sternorrhyncha in China are shown in Fig. 1. The linear regression model revealed that the ratio of observed richness to the expected richness was greater than 69.93% for all grids (Fig. 2). Therefore, our results represent relatively good sampling. It is clear that the eastern and southeastern coastal regions of mainland China, as well as Taiwan Island, have high species richness (Fig. 3A). Endemism represented by the weight of endemism showed similar distribution patterns (Fig. 3B).

Correlation analysis revealed that species richness of Sternorrhyncha was strongly correlated with NDVI, ER and PET and moderately correlated with MAT, TAR and PS (Table 1). Other environmental variables were weakly correlated with species richness. Additionally, endemism was strongly correlated with ER and TAR and moderately correlated with NDVI, PET and TS (Table 1). The remaining environmental variables were weakly correlated with endemism (Table 1).

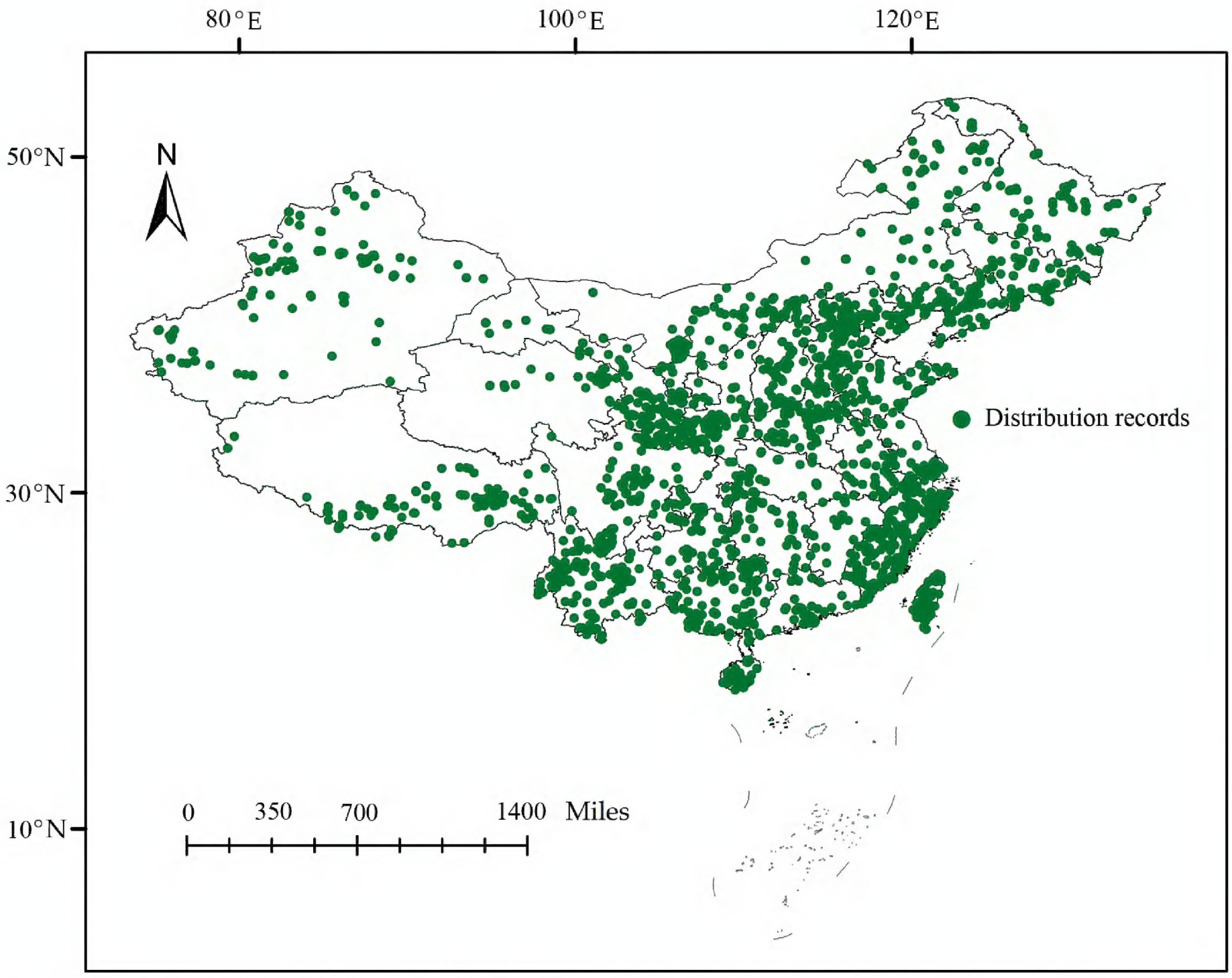

Figure 1. Distribution records of Sternorrhyncha in China.

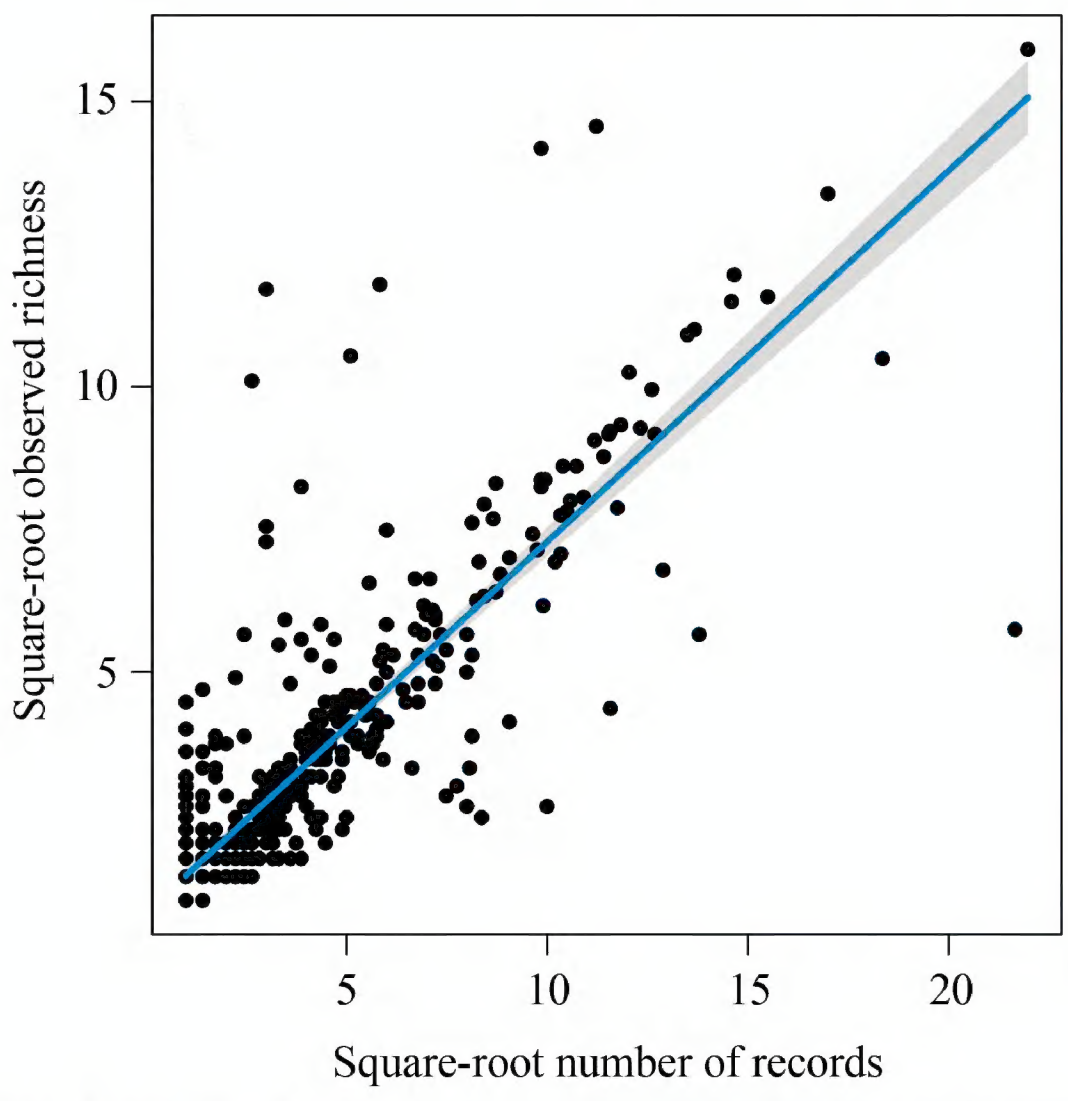

Figure 2. Linear regression (y = 0.649x + 0.781) for the square-root number of records and square-root observed richness.

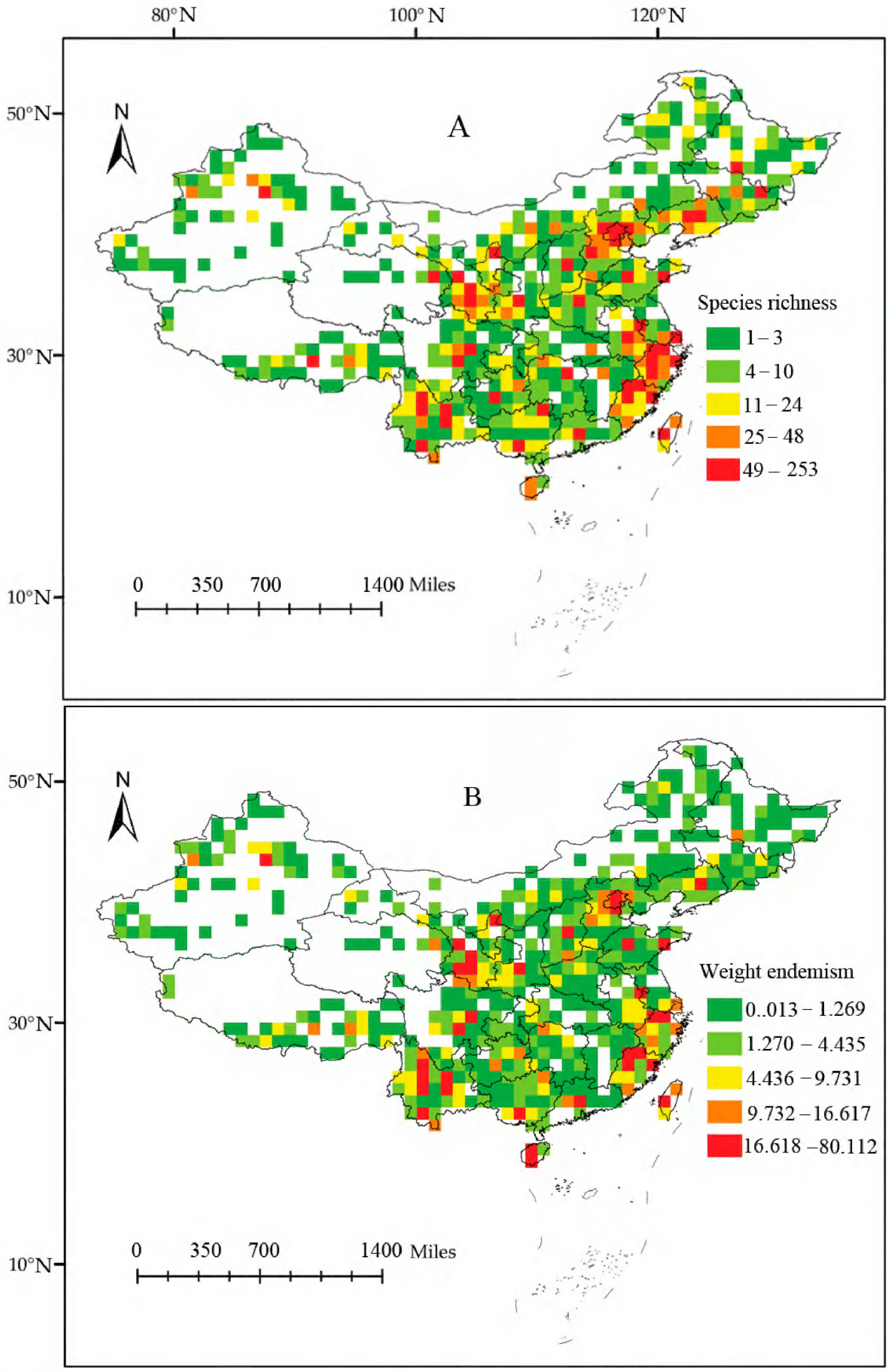

Figure 3. Species richness (**A**) and weight endemism (**B**) patterns of Sternorrhyncha in China.

The model averaging approach revealed NDVI as the most important environment variable for species richness of Sternorrhyncha, followed by PET and ER (Fig. 4A). The role of other environmental variables was relatively low. The key environment variable for endemism was found to be inconsistent with that for species richness (Fig. 4B). The importance of ER ranked first, and TAR and PET ranked second and third, respectively; the remaining variables had a relatively low effect on endemism (Fig. 4B).

Table 1. Pearson correlations between species richness/endemism of Sternorrhyncha species and environmental variables.

Environmental variables		Species richness		Endemism	
		r	*p*	*r*	*p*
Ambient energy	MAT	0.520	0.016	0.462	0.03
	PET	0.761	0.195	0.661	0.019
Water availability	MAP	0.310	0.019	0.182	0.017
	AET	0.225	0.016	0.208	0.016
Climate seasonality	TAR	−0.536	0.010	−0.736	0.002
	TS	−0.114	0.020	−0.537	0.005
	PS	0.504	0.090	−0.416	0.008
Habitat heterogeneity	ER	0.783	0.039	0.842	0.033
	SP	0.224	0.030	0.303	0.045
Productivity	NDVI	0.846	0.003	0.633	0.002
	NPP	0.349	0.002	0.271	0.014
Historical climate stability	MAT change	0.193	0.050	0.168	0.034
	MAP change	0.382	0.040	0.182	0.017

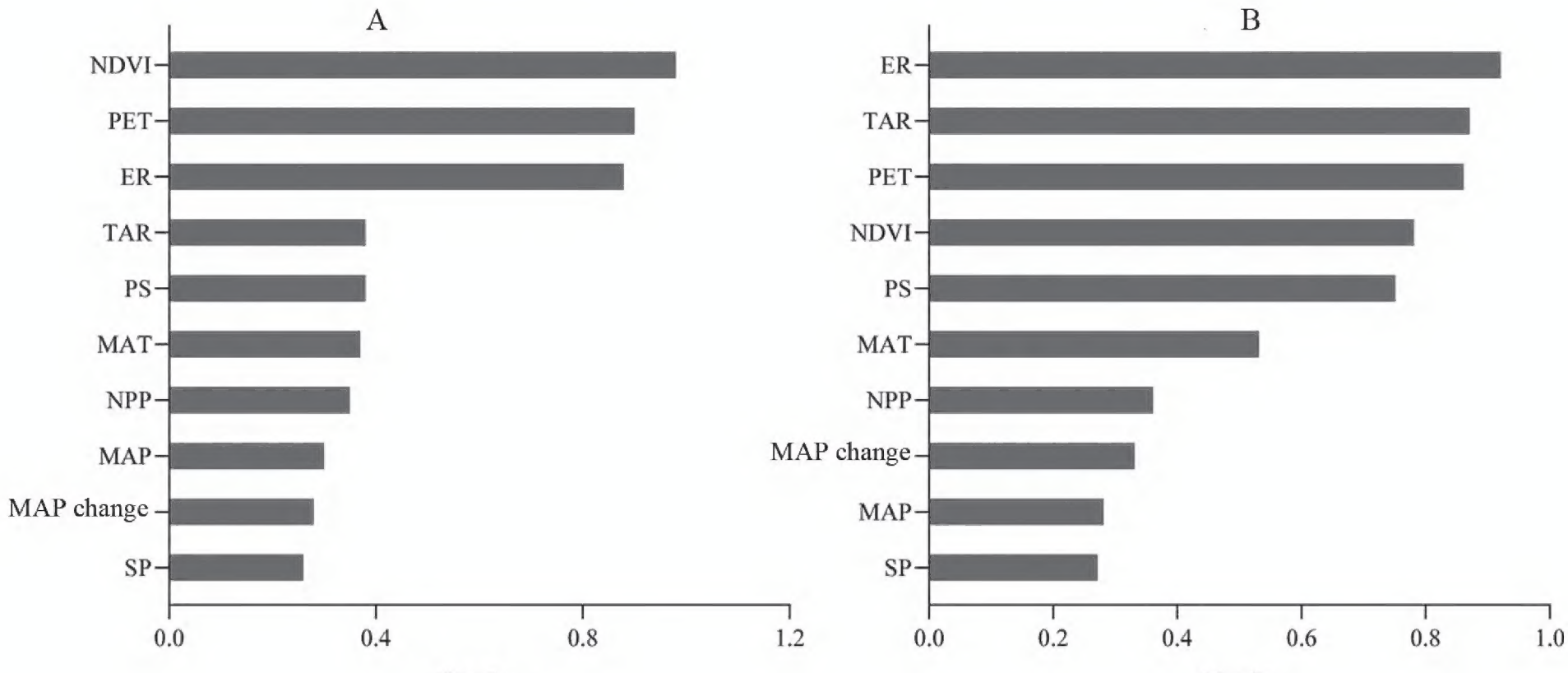

Figure 4. AIC weights of environmental variables in species richness (**A**) and endemism (**B**).

Discussion

In this study, we found that some environmental variables had a substantial impact on the formation of species richness and endemism patterns of Sternorrhyncha species. The NDVI is widely regarded as a surrogate for plant productivity and has been shown to influence broad-scale patterns of species richness in plants and animals (Mittelbach et al. 2001; Kissling et al. 2007). Our findings revealed that NDVI is the most important environmental variable in shaping the patterns of Sternorrhyncha species richness (Fig. 4), as would be expected for a phytophagous insect. Consistent with our results, previous studies on the driving factor of species diversity patterns in other phytophagous insects, for example, planthoppers (Zhao et al. 2020b), birds (Qian et al. 2009b)

and terrestrial mammals (Lin et al. 2009) in China have also found that plant productivity plays an important role. These results imply that plant productivity has become an indispensable factor that regulates patterns in species richness in China. The high species richness in a region with high plant productivity is often attributed to the increased capacity of accommodating population sizes (lower extinction rates in larger populations) in this region (Wright 1983; Evans and Gaston 2006). In this study, two surrogates of plant productivity (NPP and NDVI) were used, but NPP played a smaller role than NDVI (Fig. 4). This result differs from previous studies on other insect groups. For instance, Zhao et al. (2020b) found that NPP had a greater impact on planthopper species richness patterns in China than NDVI. Therefore, the contribution of these two environmental variables to species richness is related to taxa.

Considering the determinants of species richness patterns as the representative endemism patterns may lead to a biased understanding of the drivers of species richness patterns and hinder the development of conservation strategies (Jetz and Rahbek 2002). Therefore, the drivers of endemism patterns must be analyzed. The results of this study revealed that endemism patterns of Sternorrhyncha species are more related to topographic heterogeneity (Fig. 4). This is consistent with the viewpoint that species with a narrowing range worldwide are typically located in topographically complex regions (Jetz et al. 2004; López-Pujol et al. 2011). Several studies on insects and plants have shown that topographic heterogeneity plays a role in historical processes (i.e., as refuges), which accounts for the high correlations between topographic heterogeneity and endemism (Schuldt and Assmann 2009, 2011; López-Pujol et al. 2011). Therefore, combining our findings above, it is evident that there are differences in the mechanisms and variables that influence patterns of species richness and endemism. Additionally, this study supports that the range size of species cannot be ignored in understanding the geographic variation in species diversity. Studies have shown that endemism patterns are mostly driven by historical climate stability (Araújo et al. 2008; Rakotoarinivo et al. 2013; Zhao et al. 2020a). However, in this study, historical climate stability represented by MAP change did not dominate endemism patterns of Sternorrhyncha species, and the same was true for species richness patterns (Fig. 4).

PET, a surrogate of ambient energy, is the second and third important environmental variable for species richness and endemism patterns of Sternorrhyncha species (Fig. 4), respectively. Previous studies have reported that high ambient energy can promote species richness in a given region (Currie 1991; Qian 2013). The relative role of ambient energy and water availability in regulating species richness patterns has long been debated (Diniz-Filho et al. 2013; Xu et al. 2016; Liu et al. 2018). However, the role of these two environmental variables is closely related to the taxa and the geographical location of the region, according to a previous related study (Hawkins et al. 2003). In this study, we found that ambient energy was always more important than water availability (represented by MAP) for both species richness and endemism of Sternorrhyncha species (Fig. 4). This result may reflect that species range size does not dampen the relative importance of these two kinds of environmental variables. One of the main contributors to short-term climate stability is TAR, which in this study serves as the second important environmental variable for endemism

patterns (Fig. 4). A short-term climate stability can promote the survival of a small range of species (Klopfer 1959; Klopfer and Macarthur 1960). The study on endemism patterns of Chinese Delphacidae and Gesneriaceae also demonstrated that short-term climate stability is a main driving factor (Liu et al. 2017; Zhao et al. 2020a).

Conclusion

In summary, species richness and endemism patterns of Sternorrhyncha in China were investigated, and the relationship between environmental variables and these two kinds of species diversity patterns was further analyzed. The results showed that both species richness and endemism patterns were primarily concentrated in the eastern and southeastern coastal regions of mainland China, as well as Taiwan Island. Additionally, the predominant environmental variables for species richness and endemism patterns differed. Species richness patterns were most strongly correlated with NDVI, while endemism patterns were most strongly correlated with ER. The results highlight the importance of species range size in investigating the determinants of species diversity patterns. In this study, some important evolutionary/historical factors were not included (e.g., geological events and niche conservatism), because molecular data currently available is insufficient. Thus, once a complete phylogenetic tree using the molecular data was constructed in the future, the importance of evolutionary/historical factors can be determined.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research was funded by Scientific Research Platform of Education Department of Guizhou Province (Qianjiaoji [2022] 052), Anshun City Science and Technology Foundation (ASKN [2018]18), Anshun University Foundation (Asxyxkpt 201902), and Scientific Research Project of Education Department of Guizhou Province (Qianjiaoji [2022] 334).

Author contributions

Zhengxue Zhao: manuscript preparing, writing, and revising. Zhengxue Zhao and Xueli Feng: data analysis. Yubo Zhang, Yingjian Wang, Zhengxiang Zhou, and Tianlei Liu: distribute data collection.

Author ORCIDs

Zhengxue Zhao https://orcid.org/0000-0003-1764-8690

Data availability

All of the data that support the findings of this study are available in the main text.

References

Araújo MB, David NB, Diniz-Filho JAF, Haywood AM, Valdes PJ, Rahbek C (2008) Quaternary climate changes explain diversity among reptiles and amphibians. Ecography 31(1): 8–15. https://doi.org/10.1111/j.2007.0906-7590.05318.x

Bartón K (2018) MuMIn: Multi-Model Inference, R package version 1.43.17. https://CRAN.Rproject.org/package=MuMIn [Accessed on 15 September 2020]

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. American Naturalist 137(1): 27–49. https://doi.org/10.1086/285144

Diniz-Filho JAF, Bini LM, Hawkins BA (2003) Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography 12(1): 53–64. https://doi.org/10.1046/j.1466-822X.2003.00322.x

Diniz-Filho JAF, Rangel T, Bini LM (2008) Model selection and information theory in geographical ecology. Global Ecology and Biogeography 17(4): 479–488. https://doi.org/10.1111/j.1466-8238.2008.00395.x

Diniz-Filho JAF, De Marco Jr P, Hawkins BA (2010) Defying the curse of ignorance: Perspectives in insect macroecology and conservation biogeography. Insect Conservation and Diversity 3(3): 172–179. https://doi.org/10.1111/j.1752-4598.2010.00091.x

Diniz-Filho JAF, Ceccarelli S, Hasperué W, Rabinovich J, Leather SR, Lobo JM (2013) Geographical patterns of Triatominae (Heteroptera: Reduviidae) richness and distribution in the Western Hemisphere. Insect Conservation and Diversity 6(6): 704–714. https://doi.org/10.1111/icad.12025

Drohojowska J, Szwedo J, Ya D, Huang D, Müller P (2020) Fossils reshape the Sternorrhyncha evolutionary tree (Insecta, Hemiptera). Scientific Reports 10(1): 11390. https://doi.org/10.1038/s41598-020-68220-x

Du CC, Chen J, Jiang LY, Qiao GX (2020) High correlation of species diversity patterns between specialist herbivorous insects and their specific hosts. Journal of Biogeography 47(6): 1232–1245. https://doi.org/10.1111/jbi.13816

Dutilleul P, Clifford P, Richardson S, Hemon D (1993) Modifying the t test for assessing the correlation between two spatial processes. Biometrics 49: 305–314. https://doi.org/10.2307/2532625

Economo EP, Narula N, Friedman NR, Weiser MD, Guenard B (2018) Macroecology and macroevolution of the latitudinal diversity gradient in ants. Nature Communications 9(1): 1778. https://doi.org/10.1038/s41467-018-04218-4

Evans KL, Gaston KJ (2006) People, energy and avian species richness. Global Ecology and Biogeography 14(2): 187–196. https://doi.org/10.1111/j.1466-822X.2004.00139.x

Feng G, Mao LF, Sandel B, Swenson NG, Svenning JC (2016) High plant endemism in China is partially linked to reduced glacial-interglacial climate change. Journal of Biogeography 43(1): 145–154. https://doi.org/10.1111/jbi.12613

Gao C (2018) Species diversity pattern and underlying mechanisms for Greenideinae. PhD Thesis, Chinese Academy of Sciences, Beijing.

Gaston KJ (2000) Global patterns in biodiversity. Nature 405(6783): 220–227. https://doi.org/10.1038/35012228

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter ER, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84(12): 3105–3177. https://doi.org/10.1890/03-8006

Huston MA (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Jetz W, Rahbek C (2002) Geographic range size and determinants of avian species richness. Science 297(5586): 1548–1551. https://doi.org/10.1126/science.1072779

Jetz W, Rahbek C, Colwell RK (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. Ecology Letters 7(12): 1180–1191. https://doi.org/10.1111/j.1461-0248.2004.00678.x

Kissling WD, Rahbek C, Böhning-Gaese K (2007) Food plant diversity as broad-scale determinant of avian Frugivore richness. Proceedings of the Royal Society B, Biological Sciences 274(1611): 799–808. https://doi.org/10.1098/rspb.2006.0311

Klopfer PH (1959) Environmental determinants of faunal diversity. American Naturalist 93(873): 337–342. https://doi.org/10.1086/282092

Klopfer PH, Macarthur RH (1960) Niche size and faunal diversity. American Naturalist 94(877): 293–300. https://doi.org/10.1086/282130

Kondo TP, Gullan J, Williams DJ (2018) Coccidology. The study of scale insects (Hemiptera: Sternorrhyncha: Coccoidea). Revista Corpoica–Ciencia y Tecnología Agropecuaria 9(2): 55–61. https://doi.org/10.21930/rcta.vol9_num2_art:118

Li FS (2011) Psyllidomorpha of China (Insecta: Hemiptera). Science Press, Beijing.

Li JJ, Liu HH, Wu YX, Zeng LD, Huang XL (2019) Spatial patterns and determinants of the diversity of Hemipteran insects in the Qinghai-Tibetan Plateau. Frontiers in Ecology and Evolution 7: 165. https://doi.org/10.3389/fevo.2019.00165

Li JJ, Liu HH, Wu YX, Zeng LD, Huang XL (2021) A dataset on the diversity and geographical distributions of Hemipteran insects in China. Biodiversity Science 29(9): 1154–1158. https://doi.org/10.17520/biods.2021187

Lin X, Wang ZH, Tang ZY, Zhao SQ, Fang JY (2009) Geographic patterns and environmental correlates of terrestrial mammal species richness in China. Biodiversity Science 17(6): 652–663. https://doi.org/10.3724/SP.J.1003.2009.09065

Linder H (2001) Plant diversity and endemism in sub-Saharan tropical Africa. Journal of Biogeography 28(2): 169–182. https://doi.org/10.1046/j.1365-2699.2001.00527.x

Liu Z, Huang XL, Jiang LY, Qiao GX (2009) The species diversity and geographical distribution of aphids in China (Hemiptera, Aphidoidea). Acta Zootaxonomica Sinica 34(2): 277–291.

Liu YP, Shen ZH, Wang QG, Su XY, Zhang WJ, Shrestha N, Wang ZH (2017) Determinants of richness patterns differ between rare and common species: Implications for Gesneriaceae conservation in China. Diversity & Distributions 23(3): 235–246. https://doi.org/10.1111/ddi.12523

Liu YP, Su XY, Shrestha N, Xu XT, Wang SY, Li YQ, Wang QQ, Sandanov D, Wang ZH (2018) Effects of contemporary environment and Quaternary climate change on drylands plant diversity differ between growth forms. Ecography 42(2): 334–345. https://doi.org/10.1111/ecog.03698

Lobo JM, Lumaret JP, Jay-Robert P (2002) Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. Global Ecology and Biogeography 11(4): 265–277. https://doi.org/10.1046/j.1466-822X.2002.00291.x

López-Pujol J, Zhang FM, Sun HQ, Ying TS, Ge S (2011) Centres of plant endemism in China: Places for survival or for speciation? Journal of Biogeography 38(7): 1267–1280. https://doi.org/10.1111/j.1365-2699.2011.02504.x

Lyu YM, Wang XP, Luo JC (2020) Geographic patterns of insect diversity across China's nature reserves: The roles of niche conservatism and range overlapping. Ecology and Evolution 10(7): 3305–3317. https://doi.org/10.1002/ece3.6097

MacArthur RH (1972) Geographical ecology: patterns in the distribution of species. Harper and Row, New York.

Mittelbach GG, Scheiner SM, Steiner CF (2001) What is the observed relationship between species richness and productivity? Ecology 84(9): 2381–2396. https://doi.org/10.2307/2679922

Pennisi E (2005) What determines species diversity? Science 309(5371): 90. https://doi.org/10.1126/science.309.5731.90

Qian H (2013) Environmental determinants of woody plant diversity at a regional scale in China. PLoS ONE 8(9): e75832. https://doi.org/10.1371/journal.pone.0075832

Qian H, Kissling WD, Wang X, Andrews P (2009a) Effects of woody plant species richness on mammal species richness in southern Africa. Journal of Biogeography 36(9): 1685–1697. https://doi.org/10.1111/j.1365-2699.2009.02128.x

Qian H, Wang SL, Li YL, Wang XH (2009b) Breeding bird diversity in relation to environmental gradients in China. Acta Oecologica 35(6): 819–823. https://doi.org/10.1016/j.actao.2009.08.009

R Core Team (2019) R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna.

Rakotoarinivo M, Blach-Overgaard A, Baker WJ, Dransfield J, Moat J, Svenning JC (2013) Palaeo-precipitation is a major determinant of palm species richness patterns across Madagascar: A tropical biodiversity hotspot. Proceedings of the Royal Society B, Biological Sciences 280(1757): 20123048. https://doi.org/10.1098/rspb.2012.3048

Rangel TF, Diniz-Filho JAF, Bini LM (2010) SAM: A comprehensive application for spatial analysis in macroecology. Ecography 33(1): 46–50. https://doi.org/10.1111/j.1600-0587.2009.06299.x

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511623387

Schuldt A, Assmann T (2009) Environmental and historical effects on richness and endemism patterns of carabid beetles in the western Palaearctic. Ecography 32(5): 705–714. https://doi.org/10.1111/j.1600-0587.2009.05763.x

Schuldt A, Assmann T (2011) Belowground carabid beetle diversity in the western Palaearctic-effects of history and climate on range-restricted taxa (Coleoptera, Carabidae). ZooKeys 100: 461–474. https://doi.org/10.3897/zookeys.100.1540

Sosa V, Loera I (2017) Influence of current climate, historical climate stability and topography on species richness and endemism in Mesoamerican geophyte plants. PeerJ 5: e3932. https://doi.org/10.7717/peerj.3932

Svenning JC, Skov F (2007) Ice age legacies in the geographical distribution of tree species richness in Europe. Global Ecology and Biogeography 16(2): 234–245. https://doi.org/10.1111/j.1466-8238.2006.00280.x

Wang Z, Fang J, Tang Z, Lin X (2012) Relative role of contemporary environment versus history in shaping diversity patterns of China's woody plants. Ecography 35(12): 1124–1133. https://doi.org/10.1111/j.1600-0587.2011.06781.x

Wang F, Jiang CZ, Liu JZ, Wei JF (2017) Areas of endemism for scale insects in China. Journal of Asia-Pacific Entomology 20(4): 1170–1174. https://doi.org/10.1016/j.aspen.2017.08.024

Wei JF, Niu MM, Feng JN (2016) Diversity and distribution patterns of Scale insects in China. Annals of the Entomological Society of America 109(3): 405–414. https://doi.org/10.1093/aesa/sav159

Wei J, Li X, Lu Y, Zhao L, Zhang H, Zhao Q (2019) Modeling the potential global distribution of *Phenacoccus madeirensis* Green under various climate change scenarios. Forests 10(9): 773. https://doi.org/10.3390/f10090773

Wei J, Peng L, He Z, Lu Y, Wang F (2020) Potential distribution of two invasive pineapple pests under climate change. Pest Management Science 76(5): 1652–1663. https://doi.org/10.1002/ps.5684

Wright DH (1983) Species-energy theory: An extension of species-area theory. Oikos 41(3): 496–506. https://doi.org/10.2307/3544109

Xu XT, Wang ZH, Rahbek C, Sanders NJ, Fang JY (2016) Geographical variation in the importance of water and energy for oak diversity. Journal of Biogeography 43(2): 279–288. https://doi.org/10.1111/jbi.12620

Yan FM, Bai RE (2017) Whitefly Fauna of China. Henan Science and Technology Press, Henan.

Zhang Z, Yan Y, Tian Y, Li J, He JS, Tang ZY (2015) Distribution and conservation of orchid species richness in China. Biological Conservation 181: 64–72. https://doi.org/10.1016/j.biocon.2014.10.026

Zhao LN, Li JY, Liu HY, Qin HN (2016) Distribution, congruence, and hotspots of higher plants in China. Scientific Reports 6(1): 19080. https://doi.org/10.1038/srep19080

Zhao ZX, Jin BC, Zhou ZX, Yan L, Long JK, Chen XS (2020a) Determinants of Delphacidae richness and endemism in China. Ecological Entomology 45(6): 1396–1407. https://doi.org/10.1111/een.12924

Zhao ZX, Yang L, Long JK, Chang ZM, Zhou ZX, Zhi Y, Yang LJ, Li HX, Gong N, Wang XY, Chen XS (2020b) Testing seven hypotheses to determine what explains the current planthopper (Fulgoridae) geographical and species richness patterns in China. Insects 11(12): 892. https://doi.org/10.3390/insects11120892

Zhao ZX, Yang L, Long JK, Chang ZM, Zhou ZX, Zhi Y, Yang L, Li HX, Gong N, Wang XY, Chen XS (2021) Endemism patterns of planthoppers (Fulgoroidea) in China. Frontiers in Ecology and Evolution 9: 683722. https://doi.org/10.3389/fevo.2021.683722